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Theropod trackways as indirect evidence of pre-avian aerial behavior

T. Alexander Dececchi[a,1,2], Kyung Soo Kim[b], Martin G. Lockley[c,3], Hans C.E. Larsson[d], Thomas R. Holtz Jr.[e,f], James O. Farlow[g], and Michael Pittman[h,1,2]

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Body fossils set limits on feasible reconstructions of functional capacity and behavior in theropod dinosaurs, but do not document in-life behaviors. In contrast, trace fossils such as footprints preserve in-life behaviors that can potentially test and enhance existing reconstructions. Here, we demonstrate how theropod trackways can be used as indirect evidence of pre-avian aerial behavior, expanding the approaches available to study vertebrate flight origins. This involved exploring the behavioral implications of a two-toed Cretaceous-aged theropod trackway produced by a small, bird-like microraptorine moving at high speed. Applying first principle running biomechanics, we were able to conclude that the trackway is atypical, indirectly evidencing pre-avian aerial behavior. This trackway documents the evidence of wing-assisted aerodynamic force production during locomotion, supporting a broader distribution of this behavior than currently known. These findings support previously proposed aerial behavior in early bird-like theropods, showing how trackways will help to deepen our understanding of theropod flight origins.

trackway | feathered dinosaur | aerial behavior | flight origins

Theropod body fossils set limits on feasible reconstructions of functional capacity and behavior (1–3) but do not record in-life behaviors, whereas trace fossils can potentially test and enhance existing reconstructions (4). Theropod trackways can potentially provide indirect records of important flight behaviors including flap-running, take-off, and landing. Here, we explore this potential by reexamining one of the smallest and fastest known theropod trackways (Trackway 2) from the Lower Cretaceous (Albian) Jinju Formation of South Korea (5, 6). We considered whether these microraptorine tracks were produced under purely hindlimb power or if they also involved, at least partially, forelimb-generated aerodynamic forces. Given the suggested aerial status of microraptorines like *Microraptor* (1), this trackway is a candidate to support previously proposed aerial locomotion. We evaluate this hypothesis and discuss the significance of our results for understanding theropod locomotor evolution.

Results

Trackway 2 (Fig. 1) has an exceptional stride length to footprint length ratio of ~53 which plots as the highest ratio among our sample of 2,638 known theropod trackways (Fig. 2*A*) and 508 non-theropod trackways (Dataset S1), 139% the next highest value, 7.3 times the mean, and significantly outside the expected distribution (z test = 14.482, *P* (two tailed) = 0.00). We confirmed the 47.5 mm hip height of the trackmaker estimated by (5) using an expanded comparative dataset of microraptorine specimens (Dataset S2) under crouching and straight-leg models.

Assuming only hindlimb-driven cursorial locomotion, the trackmaker's proposed travel speed was calculated to be 10.5 m/s (37.8 km/h) (5). We calculated a corresponding Froude number of 238, ~6.7 times the next highest confirmed nonavialan theropod value (*Minisauripus zhenshuonani* Fr = 35) and much higher than living cursorial animals, including the ostrich, roadrunner, and cheetah (Fig. 1*B*; *SI Appendix*, *Extended Methods* and Dataset S3). The ground reaction forces would be comparatively immense and require skeletal strength well beyond that measured for living cursorial birds (7). Increasing the hip height estimation to total hindlimb length reduces speed and resulting Froude number to 126, still amongst the highest ever recorded and significantly higher than expected (z test = −52.514, *P* (two tailed) = 0.00).

To examine the impact of wing-assistance on stride extension and travel speed, we used data from smaller *Microraptor* specimen BMNHC PH881 (2). We found that stride length extension can produce artificially elevated speed estimates that explain the extremely high Fr values seen in Table 1. This strongly supports our assertion that Trackway 2 documents

Author affiliations: [a]Division of Natural Sciences, Dakota State University, Madison, SD 57042; [b]Department of Science Education, Chinju National University of Education, Jinju-si, Gyeongnam 52673, South Korea; [c]Dinosaur Trackers Research Group, University of Colorado Denver, Denver, CO 80217-3364; [d]Redpath Museum, McGill University, Montreal, QC H3A 0C4, Canada; [e]Department of Geology, University of Maryland, College Park, MD 20742; [f]Department of Paleobiology, National Museum of Natural History, Washington, DC 20560; [g]Department of Geosciences, Purdue University Fort Wayne, IN 46805; and [h]School of Life Sciences, The Chinese University of Hong Kong, Shatin, Hong Kong SAR, China

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[1]T.A.D. and M.P. contributed equally to this work.

[2]To whom correspondence may be addressed. Email: alex.dececchi@dsu.edu or mpittman@cuhk.edu.hk.

[3]Deceased November 25, 2023.

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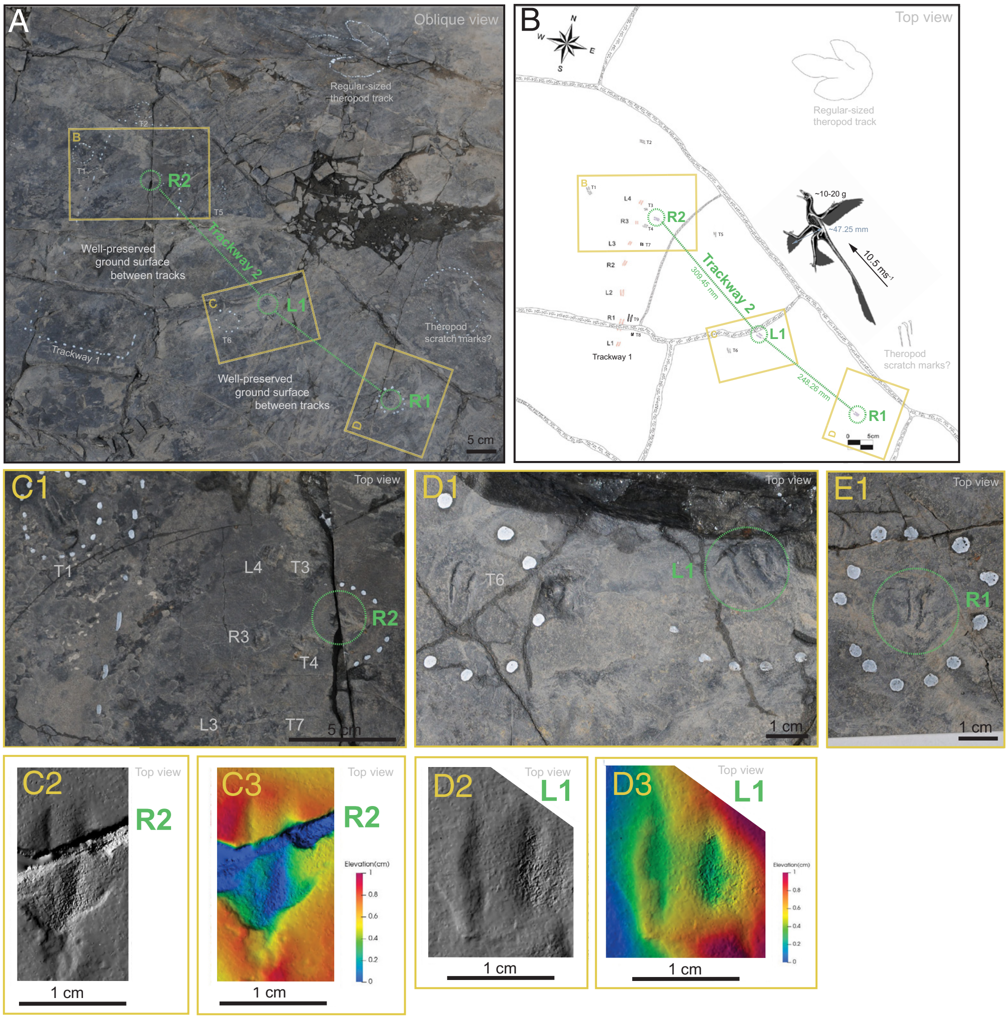

Fig. 1. Microraptorine theropod Trackway 2 from Jinju Formation of South Korea. (*A*) Trackway 2 (center; green dotted lines) in situ alongside other tracks, including Trackway 1 (*Left* side) and a single large theropod footprint (*Top Right*). (*B*) Site map accurately and faithfully illustrating footprint disposition and empty spaces on the ground. Our results suggest track making involved a behavior with both aerodynamic force production and contact with the substrate, although we cannot attribute a specific aerial behavior. Skeletal drawing by S. Hartman. (*C–E*) Distinct morphology of clearly impressed individual footprints in Trackway 2 (R1, L1, and R2). The two right prints show the same morphology (*C*2 and *E*1), which is the mirror image of the single left print (*D*2). Firsthand and photogrammetric model study of Trackway 2 (original and elevation-based coloring) allowed us to corroborate the microraptorine trackmaker (*C*2, *C*3, *D*2, *D*3, and *E*1). R1 photogrammetric model was not possible as R1 broke into pieces when Trackway 2 was lifted to save it from impending construction works. Scale bar segments are 5 cm in *A, B,* and *C*1; 1 cm in *C*2, *C*3, *D*1, *D*2, *D*3, and *E*1.

some form of wing assistance to extend stride length preserved to levels that would be impossible through running alone.

Discussion

Our results suggest that Trackway 2 records a microraptorine engaged in aerial or partially aerial behavior involving coordination between the forelimbs and hindlimbs. While we cannot make any claim linking a specific aerial behavior to the trackway (e.g., launch, landing, accelerated downward glides, or wing-assisted stride extension), we can say that track making involved a behavior featuring aerodynamic force production and contact with the substrate. The trackway therefore provides indirect support of wing-assisted behavior in action outside the lineage directly leading to birds, previously only hypothesized (1, 3, 8). This study therefore expands the approaches available for studying vertebrate flight origins.

In aerial taxa, whether powered flyers, gliders, and non-aerial adapted parachuters, they perform better with reduced body mass (9). Smaller body size lowers physical and energetic barriers to all types of aerial locomotion (2, 10), including wing-assisted aerial locomotion observed in juvenile living birds (11). Given the primitive nature of fossil paravian wing structure compared to modern birds (e.g., lack of a ligamentous pulley system) (1), size was likely a critical limitation on their flight capacity (4). This suggests specific "windows" where bouts of wing-assisted locomotion, gliding, or powered flight were accessible to maturing feathered dinosaurs whenever small body mass intersected with key parameters such as limb length and muscle volume, as in living Galliformes (11). These "windows" could vary by species, with different aerial behaviors utilized at different stages across paravian phylogeny. Thus, the origin of flight may not be a simply binary of "can or cannot" but a spectrum with different lineages utilizing aerial locomotion differently to suit their own needs.

Table 1. Effect of wing-assisted aerial behavior on stride extension in microraptorines

			Stride Length (m)			Froude number (Fr)		
	Flap angle (°)	Start speed (m/s)	no lift	Cl = 1	Cl = 1.5	no lift	Cl = 1	Cl = 1.5
Fixed wings	–	4.9*	0.77	0.83	0.89	19	25	30
	–	7.7^	1	1.33	1.6	46	118	219
Flapping wings	90	3.3#	0.6	0.84	2.6	9	25	1,112
	70	4.3#	0.71	0.99	3.09	14	44	1,976
	50	5.4#	0.81	1.12	3.54	23	67	3,115

Start speeds were based on data and methodology from (2) and based on high speed running (*), minimum stall glide speed (^), of 0.1 m/s below flapping take-off speed (#). Cl = coefficient of lift.

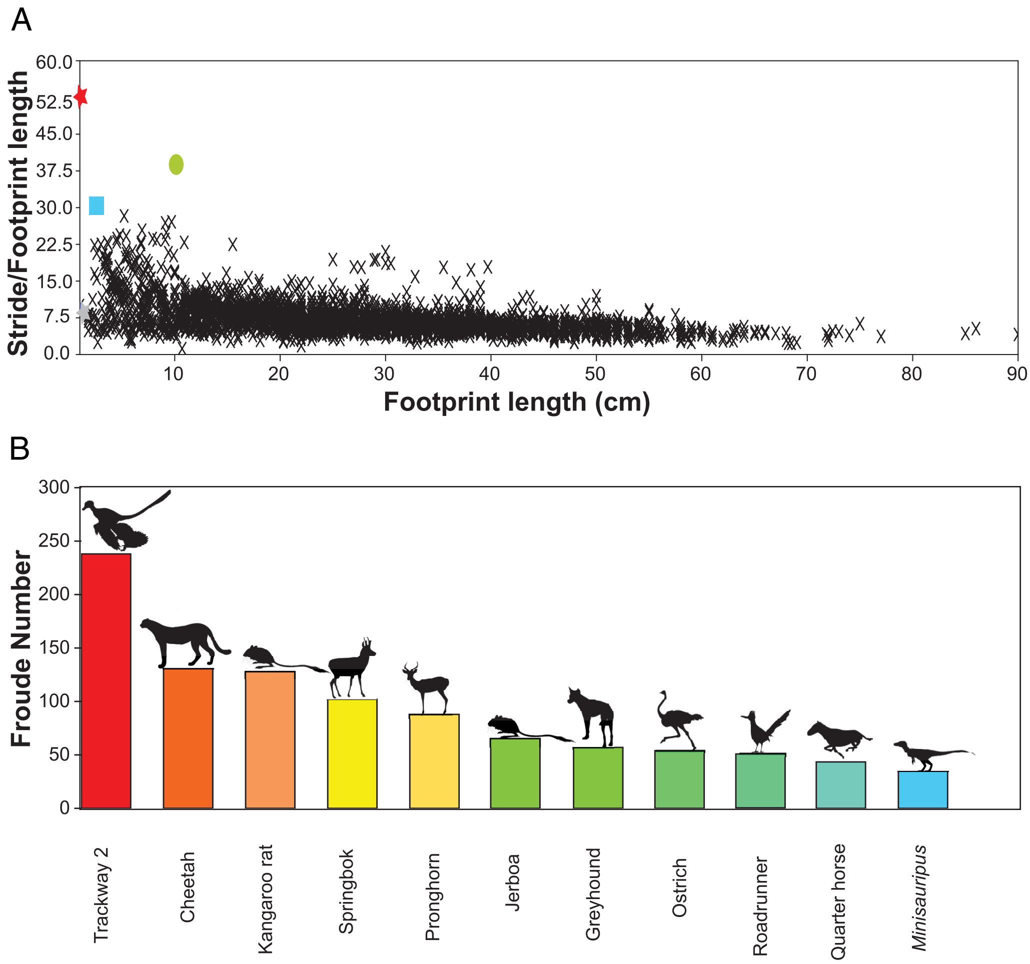

Fig. 2. Comparison of relative stride length between Trackway 2 and 2,637 other theropod trackways and between its trackmaker and extant terrestrial high-speed specialists. (*A*) Trackway 2 (red star) shows a relative stride length as a function of mean trackway footprint length in excess of any other known theropod trackway, including Trackway 1 (gray star) from the same bedding plane. The next highest confirmed theropod value from *Minisauripus* YMZ-T12 (light blue square) is included to illustrate the level of excess for Trackway 2. Relative stride length is mean trackway stride/mean trackway footprint length. Number of trackways = 2,638. Data modified from (13). (*B*) Froude number comparison for extinct and extant taxa. Trackway 2 shows a Froude number considerably higher than any extant cursorial mammal, bird, or previously documented high-speed theropod trackway (*Minisauripus*) (Dataset S3).

Materials and Methods

Trackway 2 data are based on ref. 5 and firsthand study by two original authors who are coauthors here (Fig. 1). We corroborate its assignment to *Dromaeosauriformipes rarus* [*SI Appendix*, *Extended Methods* and (5) for details]. To confirm hip height estimates (5), we used a dataset of 17 microraptorine specimens with a complete hindlimb and digit III (Dataset S2) using crouching and straight-leg models in relation to ref. 12. Assuming hind limb only locomotion, we compared relative stride length as a function of mean trackway footprint length between Trackways 1 and 2 and 2,636 other theropod trackways (Fig. 2*A*). Microraptorines had large feathered wings that could generate substantial fluid forces (2, 3, 8) so we also modeled Trackway 2 production via stride extension associated with wing-generated lift. *SI Appendix*, *Extended Methods* for details.

Data, Materials, and Software Availability. Photogrammetric model source photos data have been deposited in figshare (https://doi.org/10.6084/m9.figshare.25304638 (14); https://doi.org/10.6084/m9.figshare.25304632 (15); https://doi.org/10.6084/m9.figshare.25304650 (16); https://doi.org/10.6084/m9.figshare.25303768 (17); https://doi.org/10.6084/m9.figshare.25303756 (18); https://doi.org/10.6084/m9.figshare.25303777 (19)). All study data are included in the article and/or supporting information.

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